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MODELLING COFFEE LEAF RUST DYNAMICS TO CONTROL ITS SPREAD

CLOTILDE DJUIKEM¹, FRÉDÉRIC GROGNARD¹, ROGER TAGNE WAFO²,
SUZANNE TOUZEAU^{1,3,*} AND SAMUEL BOWONG^{2,4}

Abstract. Coffee leaf rust (CLR) is one of the main diseases that affect coffee plantations worldwide. It is caused by the fungus *Hemileia vastatrix*. Damages induce severe yield losses (up to 70%). Its control mainly relies on cultural practices and fungicides, the latter having harmful ecological impact and important cost. Our goal is to understand the propagation of this fungus in order to propose a biocontrol solution, based on a mycoparasite that inhibits *H. vastatrix* reproduction. We develop and explore a spatio-temporal model that describes CLR propagation in a coffee plantation during the rainy and dry seasons. We show the existence of a solution and prove that there exists two threshold parameters, the dry and rainy basic reproduction numbers, that determine the stability of the equilibria for the dry and rainy season subsystems. To illustrate these theoretical results, numerical simulations are performed, using a non-standard finite method to integrate the pest model. We also numerically investigate the biocontrol impact. We determine its efficiency threshold in order to ensure CLR eradication.

Mathematics Subject Classification. 35K57, 93D05, 65M06, 92D30.

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1. INTRODUCTION

Coffee is one of the most widely consumed beverages in the world; its trade satisfies the regular consumption of more than two billion people and exceeds \$10 billion worldwide [36]. Its cultivation is an important factor of social stability as it sustains the living of not less than twenty-five million small producers and their families worldwide [19]. The total production of all exporting countries in 2018 was more than 172 million 60-kilogram bags [19].

Coffee leaf rust (CLR) is a disease caused by a basidiomycete fungus, *Hemileia vastatrix*, that affects coffee trees. The fungus *H. vastatrix* is a compulsory parasite. In other words, it is a fungus that lives and develops only on coffee leaves. It attacks the lower leaves of the coffee tree and causes premature defoliation, which reduces the photosynthetic capacity and weakens the tree. Leaf fall causes abortion of a large part of the flowers and fruits, as well as desiccation of shoots. CLR is the most serious leaf disease of the coffee tree known to date [24]. It has direct and indirect economic impacts on coffee production. Direct impacts include decreased quantity

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and quality of yield. In some cases, more than 70% of the coffee production is lost [15]. Indirect impacts include increased costs to control the disease. Control methods include fungicide application [10], cultural practices [4] including stumping of diseased plants, the use of resistant cultivars [2], and biocontrol by fungal and bacterial parasites [3, 38]. These methods induce significant labor and material costs and, in the case of stumping, a year-long decline in production. To better control this fungus, it is necessary to understand the disease propagation and what conditions favor its development and dispersal.

The spread of crop diseases, in particular airborne pathogens such as fungi, has received a lot of attention from researchers. Among models that represent the pathogen spatial dispersal, one can cite the DDAL framework that focuses on the deployment of susceptible and resistant crop hosts in an agricultural landscape [27]. Fewer models represent the pathogen spread by a diffusion term in partial differential equations (PDE). For instance, Sapoukhina *et al.* also study susceptible and resistant crop mixtures for a fungal disease propagated by airborne spores in a field [31], while Burie *et al.* explore the dynamical behaviour of mildew in a vineyard [9]. These disease dynamics are relevant for CLR modelling: they include a latency period, a sporulation period, spore dispersal and germination.

CLR models in the literature represent different scales, from the individual coffee bush to the country or even the continent. Avelino *et al.* investigate the factors (coffee tree characteristics, crop management patterns, environment) that affect CLR intensity in several plots in Honduras [5]. Bebbier *et al.* determine the germination and infection risk depending on the climate in Colombia and neighbouring countries [6]. In contrast to these static approaches, Vandermeer *et al.* study the interaction between the regional and local dynamics of CLR model by representing the evolution of the proportion of infected bushes and farms [40]. Vandermeer *et al.* also represent the CLR dynamics in a coffee farm in Chiapas using an SI epidemiological model of the host [37]. In these two latter studies, the fungus life cycle is not represented. Some other models investigate CLR control. Vandermeer *et al.* look at the interaction between *H. vastatrix* and a mycoparasite *Lecanicillium lecanii* [38], while Arroyo *et al.* consider interactions with antifungal bacteria [3]. However, no existing CLR model considers *H. vastatrix* dynamics together with its interaction with the coffee host. In particular none considered the impact of CLR on berry production, which is the variable of agronomic interest.

Our aim is to understand the CLR propagation in a field and to propose a biocontrol solution based on the *Lecanicillium lecanii* mycoparasite, by a mathematical modelling approach. Biocontrol methods are still in development but could provide ecologically friendly alternatives to fungicides, which can induce pest resistance. Moreover, biocontrol can be coupled with cultural practices and does not require host replacement as for resistant plant deployment. To achieve our goal, an original CLR model is needed, based on existing crop-fungus interaction models with diffusion [9, 31] and including berry production. As coffee growth is climate-dependent and harvest is seasonal, we have to develop a hybrid spatio-temporal PDE model.

This paper is organized as follows. Section 2 is devoted to the biological background and the formulation of the spatio-temporal CLR propagation model with two seasons per year, the dry and rainy seasons. Section 3 presents the stability analysis of the subsystems during the two seasons. In Section 4, numerical simulations are performed to illustrate and validate theoretical results. We also present numerical results when mycoparasites are used to control CLR spread. Finally, we conclude the paper and propose several possible perspectives for future work.

2. COFFEE LEAF RUST DYNAMICS

2.1. Biological background

The coffee tree is a perennial plant, belonging to the Rubiaceae family, which has persistent leaves [7]. The productivity stage (flowers and fruits) begins after 3 years and lasts for 20 years on average. Flowers appear at the end of branches and require a lot of humidity for their development [18]. The annual productivity period lasts 7 to 11 months depending on coffee species and cultivars, as well as climate. In the case of Cameroon, with a single rainy period per year from April to November, there is a single harvest between November and December [34].

The life cycle of *H. vastatrix* in favorable humidity and temperature conditions lasts 5 weeks on average [41]. Urediniospores are dispersed by rain and wind. They germinate and penetrate through stomates on the underside of the leaf. This infection process requires 24 to 48 hours [25]. The first symptom is a pale yellow lesion that appears 1 to 3 weeks after infection. Sporulation, *i.e.* the production of urediniospores and teliospores, occurs 2 weeks to several months after infection [41]. A single lesion produces 4 to 6 crops of spores, releasing 300,000 to 400,000 urediniospores over a period of 3 to 5 months [25].

As most rust fungi, *H. vastatrix* produces urediniospores for asexual reproduction and teliospores for sexual reproduction. Teliospores do not infect coffee leaves and have no known host [30], so it is not established that there is an effective sexual reproduction cycle.

During the dry season, *H. vastatrix* survives primarily as mycelium in the living tissues of the coffee leaves. As infected leaves drop prematurely during the dry months, a large amount of potential inoculum for the next rainy season disappears. However, a few green leaves always persist. Moreover, urediniospores can survive about 6 weeks, so there is always some viable inoculum to infect the newly formed leaves at the start of the next rainy season [2].

2.2. Model formulation

Based on this biological knowledge, we propose a spatio-temporal coffee-CLR interaction model within a coffee plantation. We represent space and urediniospore diffusion inside a bounded domain. At each point in space, we describe the evolution of the number of coffee branches, according to their epidemiological state, based on the CLR life cycle: healthy, latent with spores germinating or non sporulating lesions, infectious with sporulating lesions, and leafless at the end of the infection process. The infection of a branch corresponds to the infection of its leaves. We consider two periods: the rainy season during which berries are produced, and the dry season. This implies that most parameters are time-dependent, as they take two values according to the season.

We obtain the following model, that is illustrated in Figure 1:

$$\left\{ \begin{array}{l} \partial_t S(t, x) = \Lambda(t) - \frac{\omega(t)\nu U(t, x)}{N(t, x)} S(t, x) - \mu(t) S(t, x), \\ \partial_t L(t, x) = \frac{\omega(t)\nu U(t, x)}{N(t, x)} S(t, x) - (\theta(t) + \mu(t)) L(t, x), \\ \partial_t I(t, x) = \theta(t) L(t, x) - (\alpha(t) + \mu(t) + d) I(t, x), \\ \partial_t J(t, x) = \alpha(t) I(t, x) - \mu(t) J(t, x), \\ \partial_t U(t, x) = \varepsilon \Delta U(t, x) + \gamma(t) I(t, x) - (\nu + \mu_U) U(t, x), \\ \partial_t B(t, x) = \delta_S(t) S(t, x) + \delta_L(t) L(t, x) + \delta_I(t) I(t, x) + \delta_J(t) J(t, x) - \mu_B B(t, x), \end{array} \right. \quad (2.1)$$

where $S(t, x)$, $L(t, x)$, $I(t, x)$, $J(t, x)$, $U(t, x)$ and $B(t, x)$ represent the densities of healthy branches, latent branches, infectious branches, leafless branches, urediniospores and berries respectively, at time t and location x defined in Ω , a simply connected bounded domain (of \mathbb{R} or \mathbb{R}^2) with smooth boundary $\partial\Omega$. The densities are $/m$ or $/m^2$ depending on the choice of Ω . The total density of branches is $N(t, x) = S(t, x) + L(t, x) + I(t, x) + J(t, x)$.

The recruitment of healthy branches occurs at rate $\Lambda(t)$. Urediniospores are deposited on leaves of all branches at rate ν and a fraction S/N lands on healthy branches. These spore covered healthy branches become latent branches with rate $\omega(t)$, which represents the germination efficacy, that is the number of healthy branches which become latent branches, per deposited spore. The latent branches become infectious at rate $\theta(t)$, where $1/\theta(t)$ corresponds to the latency period, and in turn become leafless branches at rate $\alpha(t)$, where $1/\alpha(t)$ corresponds to the sporulation period. All branches undergo natural mortality with baseline rate $\mu(t)$ and the infectious branches have an additional constant mortality rate d due to the disease. Urediniospores are produced by infectious branches at rate $\gamma(t)$ and lose their ability to infect coffee branches at constant rate μ_U . Parameter

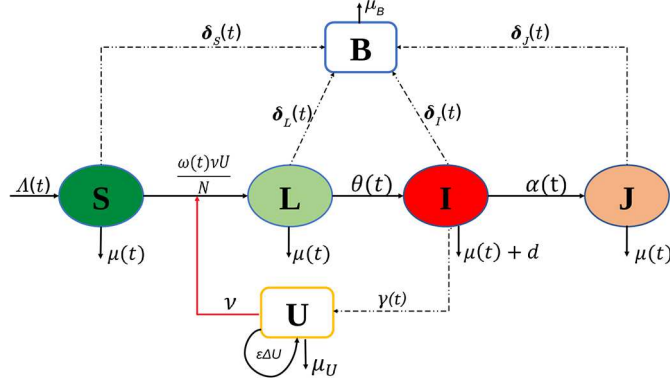


FIGURE 1. Diagram of the CLR propagation model in the coffee plantation corresponding to system (2.1). State variables are: healthy branches (S), latent branches (L), infectious branches (I), leafless branches (J), urediniospores (U) and berries (B). $\varepsilon\Delta U$ corresponds to urediniospore diffusion.

ε is the urediniospore diffusion coefficient. Berries are produced by all types of branches at different rates: $\delta_S(t) \geq \delta_L(t) \geq \delta_I(t) \geq \delta_J(t)$. They have a constant mortality rate μ_B . All parameters are assumed to be non negative.

Having two seasons, let us consider T the yearly period and τ the duration of the dry season. We set the initial time $t = 0$ at the beginning of a dry season. Then, for n years, we assume that time-dependent parameters $m(t)$, where $m(t) \in \{\Lambda(t), \omega(t), \theta(t), \alpha(t), \gamma(t), \mu(t)\}$, and $\delta_i(t)$, with $i \in \{S, L, I, J\}$, are constant during each season and can be written as follows:

$$m(t) = \begin{cases} m_D & \text{for } t \in [nT, nT + \tau[, \\ m_R & \text{else,} \end{cases} \quad \text{and} \quad \delta_i(t) = \begin{cases} 0 & \text{for } t \in [nT, nT + \tau[, \\ \bar{\delta}_i & \text{else,} \end{cases} \quad (2.2)$$

where D represents the dry season and R the rainy season.

Table 1 summarizes the biological meaning of parameter values for system (2.1).

Initial conditions are $(\phi_S(x), \phi_L(x), \phi_I(x), \phi_J(x), \phi_U(x)) \in (L^2(\Omega))^5$ where

$$\begin{cases} S(0, x) = \phi_S(x) > 0, & L(0, x) = \phi_L(x) \geq 0, & I(0, x) = \phi_I(x) \geq 0, \\ J(0, x) = \phi_J(x) \geq 0, & U(0, x) = \phi_U(x) \geq 0, & \forall x \in \Omega. \end{cases} \quad (2.3)$$

with $B(0, x) = 0 \forall x \in \Omega$. We assume that the harvest occurs instantaneously at the end of each rainy season. Thus $B(t, x)$ is brought back to 0 at $t = nT$, with other variables unchanged.

We suppose that the domain Ω is isolated, which implies that spores do not get in or out and that there is no interaction with the outside environment. To ensure this property, we assume that there is a large enough buffer zone without coffee plants around the coffee plantation (hence around the domain Ω), so that no urediniospores are introduced from outside the plantation. Moreover, we neglect the spores that could potentially get out of the plantation. This absence of transfer is classically represented through the homogeneous Neumann boundary:

$$\frac{\partial U}{\partial \eta} = 0, \quad \text{on } \partial\Omega \quad (2.4)$$

where η denotes the unit outward normal on $\partial\Omega$.

TABLE 1. Description of parameters for system (2.1) – numerical values are used in Section 4.

Symbol	Biological meaning	Value		Source
		Dry season (D)	Rainy season (R)	
Λ_p	Recruitment rate	6 day ⁻¹	8 day ⁻¹	Assumed
ω_p	Inoculum effectiveness	4.5%	5.5%	[29]
$\bar{\delta}_S$	Production rate of berries by S	0	0.7 day ⁻¹	[13, 19]
$\bar{\delta}_L$	Production rate of berries by L	0	0.5 day ⁻¹	[13, 19]
$\bar{\delta}_I$	Production rate of berries by I	0	0.3 day ⁻¹	[13, 19]
$\bar{\delta}_J$	Production rate of berries by J	0	0.05 day ⁻¹	[13, 19]
$1/\theta_p$	Latency period duration	30 days	21 days	[41]
μ_p	Mortality of mature branches	0.0134 day ⁻¹	0.0034 day ⁻¹	Assumed
$1/\alpha_p$	Sporulation period duration	150 days		[41]
γ_p	Production rate of urediniospores	$\in [0, 20]$ day ⁻¹		[8]
μ_B	Mortality rate of berries	0.0021 day ⁻¹		Assumed
d	Mortality rate due to the disease	0.056 day ⁻¹		Assumed
ε	Diffusion coefficient	5000 m ² day ⁻¹		[9]
ν	Deposition rate	0.09 day ⁻¹		[8]
μ_U	Mortality rate of urediniospores	0.015 day ⁻¹		[44]

Remark 2.1. When considered in one dimension, the space domain simply is an interval $\Omega = [x_{\min}, x_{\max}]$, whose boundary as considered in (2.4) is the pair of points $\partial\Omega = \{x_{\min}, x_{\max}\}$, and condition (2.4) becomes $\frac{\partial U}{\partial x} = 0$ in $x = x_{\min}$ and $x = x_{\max}$.

3. MATHEMATICAL ANALYSIS

Herein, we present the basic properties of the subsystems of system (2.1), defined over each season. For any parameter m , we denote by m_p the seasonal constant value of the parameter m where $p = R$ for the rainy season and $p = D$ for the dry season. Replacing the value of every parameter $m(t)$ of system (2.1), with the corresponding constant value m_p with respect to the season, and removing the $\partial_t B$ equation since B is not present in the other equations of system (2.1), we obtain:

$$\left\{ \begin{array}{l} \partial_t S = \Lambda_p - \frac{\omega_p \nu U}{N} S - \mu_p S, \\ \partial_t L = \frac{\omega_p \nu U}{N} S - (\theta_p + \mu_p) L, \\ \partial_t I = \theta_p L - (\alpha_p + \mu_p + d) I, \\ \partial_t J = \alpha_p I - \mu_p J, \\ \partial_t U - \varepsilon \Delta U = \gamma_p I - (\nu + \mu_U) U, \\ \frac{\partial U}{\partial \eta} = 0, \quad \text{on } \partial\Omega, \\ S(0, x) = \phi_S, L(0, x) = \phi_L, I(0, x) = \phi_I, J(0, x) = \phi_J, U(0, x) = \phi_U, \forall x \in \Omega. \end{array} \right. \quad (3.1)$$

3.1. Basic properties

In this section, we will first establish positivity of the solutions if they exist in Lemma 3.2, their boundedness in Lemma 3.3, and finally their existence and uniqueness in Lemma 3.6. Through these, we obtain positivity, boundedness and global existence of solutions of subsystem (3.1) in Theorem 3.7.

In order to show positivity, we will be using the following lemma of [26].

Lemma 3.1 ([26]). Suppose $w \in C([0, \mathcal{T}] \times \bar{\Omega}) \cap C^{1,2}((0, \mathcal{T}) \times \Omega)$ that satisfies:

$$\begin{cases} w_t - D\Delta w \geq -c(t, x)w(t, x), & x \in \Omega, \quad 0 < t \leq \mathcal{T}, \\ \frac{\partial w}{\partial \eta} \geq 0, & \text{on } \partial\Omega, \\ w(0, x) \geq 0, & x \in \Omega, \end{cases}$$

where $c(t, x)$ is any bounded function in $[0, \mathcal{T}] \times \Omega$. Then, $w(t, x) \geq 0$ on $[0, \mathcal{T}] \times \bar{\Omega}$. Moreover, $w(t, x) > 0$ or $w \equiv 0$ in $(0, \mathcal{T}) \times \Omega$.

Since the initial values are non-negative and the growth functions on the right-hand side of system (3.1) are assumed to be sufficiently smooth in \mathbb{R}_+^5 , we have the following result over the positivity of a solution of subsystems (3.1), if it exists:

Lemma 3.2. Any solution $(S(t, x), L(t, x), I(t, x), J(t, x), U(t, x)) \in [C([0, \mathcal{T}_{\max}) \times \bar{\Omega}) \cap C^{1,2}((0, \mathcal{T}_{\max}) \times \Omega)]^5$ of subsystems (3.1) is positive over $[0, \mathcal{T}_{\max})$, the largest interval over which the solution of subsystems (3.1) exists.

Proof. For the positivity of S, L, I, J , let us define the supremum $t_1 = \sup \{t > 0, S(t, x) > 0, L(t, x) > 0, I(t, x) > 0, J(t, x) > 0, U(t, x) > 0 \forall x \in \Omega\}$, and suppose $t_1 < \mathcal{T}_{\max}$.

Using the definition of supremum, there does not exist $t \in [0, t_1)$ and $x \in \Omega$ such that any variable is equal to zero.

Among S, L, I, J, U , let us first consider S to be the variable such that there exists x with $S(t_1, x) = 0$, and let us define:

$$\lambda(t, x) = \exp \left(\int_0^t \frac{\omega_p \nu U(a, x)}{N(a, x)} da + \mu_p t \right).$$

One has:

$$\begin{aligned} \partial_t(\lambda(t, x)S(t, x)) &= \lambda(t, x) \left[\partial_t S(t, x) + \frac{\omega_p \nu U}{N} S(t, x) + \mu_p S(t, x) \right] \\ &= \Lambda_p \lambda(t, x) \\ &> 0 \end{aligned}$$

where Λ_p is obtained from the expression of $\partial_t S(t, x)$ in subsystems (3.1). By integration of this expression over $[0, t_1]$, we obtain:

$$S(t_1, x)\lambda(t_1, x) - \phi_S(x)\lambda(0, x) > 0.$$

Since $\lambda(t_1, x) > 0$ and $\phi_S(x)\lambda(0, x) > 0$, we have $S(t_1, x) > 0$, which contradicts the hypothesis that $S(t_1, x) = 0$. Hence $S(t, x) > 0$ for all $(t, x) \in [0, t_1] \times \Omega$.

Also, the $\partial_t L$, $\partial_t I$ and $\partial_t J$ equations are linear scalar equations with forcing terms $\frac{\omega_p \nu U}{N} S$, $\theta_p L$ and $\alpha_p I$ that are positive over the interval $[0, t_1]$; hence $L(t_1, x)$, $I(t_1, x)$ and $J(t_1, x)$ are positive.

Hence, if $t_1 < \mathcal{T}_{\max}$ as we supposed, we must have, for some x , $U(t_1, x) = 0$.

As $I(t, x) > 0$ over $[0, t_1]$, the last equation of subsystems (3.1) then gives rise to the following inequality system:

$$\begin{cases} \partial_t U - \varepsilon \Delta U \geq -(\nu + \mu_U)U, & (t, x) \in (0, t_1] \times \Omega \\ \frac{\partial U}{\partial \eta} \geq 0 & \text{on } \partial\Omega, \\ U(0, x) \geq 0, & \forall x \in \Omega. \end{cases} \quad (3.2)$$

Since $\nu + \mu_U$ is bounded in $[0, t_1] \times \Omega$, it follows from Lemma 3.1 that $U(t, x) > 0$ in $[0, t_1] \times \Omega$. This contradicts $U(t_1, x) = 0$, and hence the assumption $t_1 < \mathcal{T}_{\max}$. Therefore all variables are positive for all times smaller than \mathcal{T}_{\max} .

This achieves the proof. \square

Lemma 3.3. *Let $(S, L, I, J, U) \in C^0([0, \mathcal{T}_{\max}) \times \bar{\Omega}) \cap C^{1,2}([0, \mathcal{T}_{\max}) \times \Omega)$ ⁵ be the solution of subsystems (3.1) with bounded initial conditions. Then this solution is bounded, $\mathcal{T}_{\max} = +\infty$, $0 < N(t, x) = S + L + I + J \leq N_m$ and $0 < U(t, x) \leq U_m$, where:*

$$N_m = \max \left\{ \frac{\Lambda_p}{\mu_p}, \|\phi\|_\infty \right\} \quad \text{and} \quad U_m = \max \left\{ \max\{\Lambda_p/\mu_p, \|\phi\|_\infty\} \frac{\gamma_p}{(\nu + \mu_U)}, \|\phi_U\|_\infty \right\}.$$

Proof. Let $\phi(x) = \phi_S(x) + \phi_L(x) + \phi_I(x) + \phi_J(x)$. The N -dynamics then satisfy:

$$\begin{cases} \partial_t N \leq \Lambda_p - \mu_p N, & (t, x) \in [0, \mathcal{T}_{\max}) \times \Omega \\ N(0, x) = \phi(x) \leq \|\phi\|_\infty = \max_{x \in \Omega} \phi(x). \end{cases} \quad (3.3)$$

upon which we build the upper-bounding system

$$\begin{cases} \frac{dW_1}{dt} = \Lambda_p - \mu_p W_1, \\ W_1(0) = \|\phi\|_\infty. \end{cases} \quad (3.4)$$

The comparison principle then yields:

$$N(t, x) \leq W_1(t) = \frac{\Lambda_p}{\mu_p} + \left(\phi(x) - \frac{\Lambda_p}{\mu_p} \right) e^{-\mu_p t}$$

for all $(t, x) \in [0, \mathcal{T}_{\max}) \times \Omega$. Since $W_1(t) \leq \max\{\frac{\Lambda_p}{\mu_p}, \|\phi\|_\infty\}$ for $t \in [0, \infty)$, one has that $N(t, x)$ stays bounded and is hence defined for all times:

$$0 < N(t, x) \leq \max \left\{ \frac{\Lambda_p}{\mu_p}, \|\phi\|_\infty \right\} = N_m, \quad \forall (t, x) \in [0, \infty) \times \Omega.$$

This upper-bound also holds for S , L , I and J which are integral parts of N .

From the upper-bound on I and the last equation of subsystems (3.1), we can deduce that:

$$\begin{cases} \partial_t U - \varepsilon \Delta U \leq \max\{\Lambda_p/\mu_p, \|\phi\|_\infty\} \gamma_p - (\nu + \mu_U)U, & (t, x) \in [0, \mathcal{T}_{\max}) \times \Omega \\ U(0, x) = \phi_U(x) \leq \|\phi_U\|_\infty = \max_{x \in \Omega} \phi_U(x), \\ \frac{\partial U}{\partial \eta} = 0, & x \in \partial\Omega, \end{cases} \quad (3.5)$$

and the upper-bounding system:

$$\begin{cases} \frac{dW_2}{dt} = \max\{\Lambda_p/\mu_p, \|\phi\|_\infty\} \gamma_p - (\nu + \mu_U)W_2, \\ W_2(0) = \|\phi_U\|_\infty. \end{cases} \quad (3.6)$$

It then follows that for all $(t, x) \in [0, \mathcal{T}_{\max}) \times \Omega$:

$$U(t, x) \leq W_2(t) = \max\{\Lambda_p/\mu_p, \|\phi\|_\infty\} \frac{\gamma_p}{(\nu + \mu_U)} + \left(\phi_U(x) - \max\{\Lambda_p/\mu_p, \|\phi\|_\infty\} \frac{\gamma_p}{(\nu + \mu_U)} \right) e^{-(\nu + \mu_U)t}.$$

Hence, as was done for N , we have:

$$U(t, x) \leq \max \left\{ \max\{\Lambda_p/\mu_p, \|\phi\|_\infty\} \frac{\gamma_p}{(\nu + \mu_U)}, \|\phi_U\|_\infty \right\} = U_m, \quad \forall (t, x) \in [0, \infty) \times \Omega.$$

This completes the proof \square

Now we prove existence and uniqueness of a local solution of subsystems (5). The idea is to write the system in the abstract form on a suitable Hilbert space and then to use the Hille-Yosida Theorem to conclude

We therefore introduce the linear space $\mathbf{H} = (\mathbf{L}^2(\Omega))^5$ endowed with the usual inner product:

$$\|(y, z)\|_{\mathbf{H}} = \sum_{i=1}^5 (y_i, z_i)_{\mathbf{L}^2(\Omega)}, \quad y = (y_1, y_2, y_3, y_4, y_5), \quad z = (z_1, z_2, z_3, z_4, z_5);$$

\mathbf{H} is a Hilbert space. Now define on \mathbf{H} the linear operator A such that:

$$Ay = (\mu_p y_1, \mu_p y_2, \mu_p y_3, \mu_p y_4, -\varepsilon \Delta y_5), \quad (3.7)$$

with domain $D(A) = (\mathbf{L}^2(\Omega))^4 \times H_\eta^2(\Omega)$, where $H_\eta^2(\Omega) := \{u \in H^1(\Omega), \Delta u \in \mathbf{L}^2(\Omega), \frac{\partial u}{\partial \eta} = 0\}$

Remark 3.4. For $u \in H_\eta^2(\Omega)$ the boundary condition $\frac{\partial u}{\partial \eta} = 0$ implies that

$$\forall v \in H^1(\Omega), \quad \int_\Omega -\Delta u v \, dx = \int_\Omega \nabla u \cdot \nabla v \, dx. \quad (3.8)$$

We will need the following result.

Lemma 3.5 ([28]). *Let ε be a positive real number. Let $f \in L^2(\Omega)$ and g the trace on $\partial\Omega$ of an element of $H^1(\Omega)$. Assume that Ω is a bounded subset of \mathbb{R}^N , $N = 1, 2$ with smooth boundary and consider the following stationary boundary value problem:*

$$\begin{cases} u - \varepsilon \Delta u = f & \text{a.e. on } \Omega, \\ \frac{\partial u}{\partial \eta} = g & \text{a.e. on } \partial\Omega. \end{cases} \quad (3.9)$$

Then, the problem (3.9) has a unique solution $u \in H^1(\Omega)$. Moreover u belongs to $H^2(\Omega)$ and there exists a universal constant $M > 0$ that only depends on ε , N and Ω such that

$$\|u\|_{H^1(\Omega)} \leq M(\|f\|_{L^2(\Omega)} + \|g\|_{L^2(\partial\Omega)}).$$

We have the following result about the existence of solution of subsystems (3.1).

Lemma 3.6. *Assume that the initial conditions (2.3) holds, then there exists a unique local solution of problem (3.1) defined on $[0, \mathcal{T}_{\max}) \times \Omega$. More precisely:*

$$(S, L, I, J, U) \in C((0, \mathcal{T}_{\max}); D(A)) \cap C([0, \mathcal{T}_{\max}); \mathbf{H}) \cap C^1((0, \mathcal{T}_{\max}); \mathbf{H});$$

Moreover,

$$(S, L, I, J, U) \in [C([0, \mathcal{T}_{\max}) \times \bar{\Omega}) \cap C^{1,2}((0, \mathcal{T}_{\max}) \times \Omega)]^5 \text{ if } (\phi_S, \phi_L, \phi_I, \phi_J, \phi_U) \in (C(\Omega))^4 \times L^2(\Omega).$$

Proof. System (3.1)–(2.3) can be written abstractly in the Hilbert space \mathbf{H} in the following form:

$$\begin{cases} y'(t) = Ay(t) + F(y(t)), & t \geq 0, \\ y(0) = y_0 \in D(A), \end{cases} \quad (3.10)$$

where $y = (S, L, I, J, U)$, $y_0 = (\phi_S, \phi_L, \phi_I, \phi_J, \phi_U)$, Ay is defined as in equation (3.7) and:

$$F(y) = \left(\Lambda_p - \frac{\omega_p \nu U}{N} S, \frac{\omega_p \nu U}{N} S - \theta_p L, \theta_p L - (\alpha_p + d)I, \alpha_p I, \gamma_p I - (\nu + \mu_U)U \right).$$

Note that, since Ω is bounded, for $y = (S, L, I, J, U) \in \mathbf{H}$, one has $F(y) \in \mathbf{H}$. Now let us show that the linear operator A is a maximal monotone operator on \mathbf{H} .

- $\forall v \in D(A)$, $(Av, v) = \sum_{i=1}^4 \|v_i\|_{L^2}^2 - \varepsilon \int_{\Omega} \Delta u_5 u_5 dx$. Since $u_5 \in H_{\eta}^2(\Omega)$, the identity (3.8) is satisfied with $v = u_5$ and one obtains that:

$$(Av, v) = \sum_{i=1}^4 \|v_i\|_{L^2}^2 + \varepsilon \int_{\Omega} |\nabla u_5|^2 dx \geq 0,$$

which implies that A is monotone.

- Now, let us show that $\forall v \in D(A)$, $\exists u \in \mathbf{H}$, $u + Au = v$. Let $v = (v_1, v_2, v_3, v_4, v_5) \in D(A)$. We are looking for $u = (u_1, u_2, u_3, u_4, u_5) \in D(A)$, such that $u + Au = v$. With this in mind, one has:

$$u + Au = v \iff (1 + \mu_p)u_i = v_i, \quad i = 1, \dots, 4 \quad \text{and} \quad \begin{cases} u_5 - \varepsilon \Delta u_5 = v_5 & \text{in } \Omega, \\ u_5 \in H_{\eta}^2(\Omega). \end{cases}$$

Therefore, for $i = 1, \dots, 4$, $u_i = \frac{1}{1 + \mu_p} v_i \in L^2(\Omega)$ and one obtains u_5 by solving the following elliptic problem:

$$\begin{cases} u_5 - \varepsilon \Delta u_5 = v_5 & \text{in } \Omega, \\ \frac{\partial u_5}{\partial \nu} = 0 & \text{on } \partial\Omega. \end{cases} \quad (3.11)$$

According to Lemma 3.5, there exists a unique $u_5 \in H_{\eta}^2(\Omega)$ solution of (3.11) and A is maximal. By the Hille-Yosida theorem [28], we conclude that $-A$ is the infinitesimal generator of a C_0 semigroup of contractions on \mathbf{H} .

- We now show that F is Lipschitz continuous in both variables. Let $y = (S, L, I, J, U)$, $\tilde{y} = (\tilde{S}, \tilde{L}, \tilde{I}, \tilde{J}, \tilde{U}) \in \mathbf{H}$. Therefore, one has:

$$\begin{aligned} F(y) - F(\tilde{y}) = & \left(\omega_p \nu \left(-\frac{U}{N} S + \frac{\tilde{U}}{\tilde{N}} \tilde{S} \right), \omega_p \nu \left(\frac{U}{N} S - \frac{\tilde{U}}{\tilde{N}} \tilde{S} \right) - \theta_p (L - \tilde{L}), \right. \\ & \left. \theta_p (L - \tilde{L}) - (\alpha_p + d)(I - \tilde{I}), \alpha_p (I - \tilde{I}), \gamma_p (I - \tilde{I}) - (\nu + \mu_U)(U - \tilde{U}) \right). \end{aligned}$$

Since $\dot{N} = \Lambda_p - \mu_p N - dI \geq \Lambda_p - \mu_p N - dN$, we have $N(t, x) \geq \min(\frac{\Lambda_p}{\mu_p + d}, \tilde{\phi}(x))$. Moreover, according to Lemma 3.3, \tilde{U} is bounded. This implies that $\frac{\tilde{U}}{N}$ is bounded. Similarly, $\frac{\tilde{U}}{N}$ is bounded. As $\frac{S}{N} \leq 1$, from the identity $\frac{U}{N}S - \frac{\tilde{U}}{N}\tilde{S} = \frac{U-\tilde{U}}{N}S - \frac{\tilde{U}}{N}(\tilde{S} - S) + \frac{\tilde{U}S}{NN}(\tilde{N} - N)$, we obtain:

$$\|F(y) - F(\tilde{y})\|_{\mathbf{H}} \leq K\|y - \tilde{y}\|_{\mathbf{H}},$$

where K is a constant that depends on the constant $\omega_p, \nu, \theta_p, \alpha_p, d, \gamma_p$ and μ_U . Thus F is uniformly Lipschitz continuous on \mathbf{H} . Using the fact that the solution are positive, we can now apply Theorem 1.6 page 189 of [28] and conclude that system (3.10) has a unique local strong solution on $[0, \mathcal{T}_{\max})$ in the sense that $(S, L, I, J, U) \in C((0, \mathcal{T}_{\max}); D(A)) \cap C([0, \mathcal{T}_{\max}); \mathbf{H}) \cap C^1((0, \mathcal{T}_{\max}); \mathbf{H})$, we can also use the method present in [43] to conclude prove. This completes the proof. \square

Theorem 3.7. *Subsystems (3.1), with initial conditions in \mathbf{H} that verify $0 < \phi_S + \phi_L + \phi_I + \phi_J \leq N_m$, $0 \leq \phi_U \leq U_m$ for all $x \in \bar{\Omega}$, admit a unique global solution in $C((0, \infty); D(A)) \cap C([0, \infty); \mathbf{H}) \cap C^1((0, \infty); \mathbf{H})$ such that, for all $(t, x) \in \mathbb{R}_+ \times \Omega$*

$$S(t, x) > 0, \quad L(t, x) > 0, \quad I(t, x) > 0, \quad J(t, x) > 0, \quad 0 < N(t, x) \leq N_m, \quad 0 < U(t, x) \leq U_m$$

where $N_m = \max\left\{\frac{\Lambda_p}{\mu_p}, \|\phi\|_{\infty}\right\}$ and $U_m = \max\left\{\max\{\Lambda_p/\mu_p, \|\phi\|_{\infty}\} \frac{\gamma_p}{(\nu + \mu_U)}, \|\phi_U\|_{\infty}\right\}$

Proof. Using Lemma 3.2, Lemma 3.3 and Lemma 3.6 we conclude the existence and uniqueness of bounded positive solution of subsystems (3.1) defined on $[0, \infty) \times \Omega$. we can conclude the proof of this theorem \square

3.2. Equilibria and their stability

Here, we compute the equilibria of subsystems (3.1) with $p = D$ or R and study their stability. Let

$$\mathcal{R}_0^{(p)} = \frac{\gamma_p}{(\nu + \mu_U)} \frac{\nu \omega_p}{(\theta_p + \mu_p)} \frac{\theta_p}{(\alpha_p + \mu_p + d)}$$

The expression $\mathcal{R}_0^{(p)}$ is derived in (A.6) in the proof of the local stability of the disease free equilibrium. It corresponds to the basic reproduction number in the dry ($p = D$) or rainy ($p = R$) season, since (i) $\frac{\gamma_p}{(\nu + \mu_U)}$ represents the mean number of new urediniospores generated by a single infectious branch and (ii) $\frac{\nu \omega_p}{(\theta_p + \mu_p)} \frac{\theta_p}{(\alpha_p + \mu_p + d)}$ measures the average number of new infectious branches generated by a single urediniospore introduced in a completely susceptible field. We prove the following results for the stability of equilibria of subsystems (3.1).

Lemma 3.8.

- If $\mathcal{R}_0^{(p)} < 1$ the disease-free equilibrium (DFE) $Q_p^0 = \left(\frac{\Lambda_p}{\mu_p}, 0, 0, 0, 0\right)$ is locally asymptotically stable (LAS).
- If $\mathcal{R}_0^{(p)} > 1$ and close to one, the DFE is unstable and there exists a unique positive endemic equilibrium $Q_p^* = (S_p^*, I_p^*, J_p^*, U_p^*)$, where

$$I_p^* = \frac{\Lambda_p(\nu + \mu_U)(\mathcal{R}_0^{(p)} - 1)}{\gamma_p \omega_p \nu - d(\nu + \mu_U)}, \quad S_p^* = \frac{\Lambda_p - dI_p^*}{\mu_p \mathcal{R}_0^{(p)}}, \quad L_p^* = \frac{(\alpha_p + \mu_p + d)}{\theta_p} I_p^*, \quad J_p^* = \frac{\alpha_p}{\mu_p} I_p^* \quad \text{and} \quad U_p^* = \frac{\gamma_p}{(\nu + \mu_U)} I_p^* \quad (3.12)$$

which is locally asymptotically stable.

Proof. The proof is given in Appendix. \square

Using Lyapunov theory and LaSalle's principle [21], we prove the global stability of the DFE, which implies that the CLR will dwindle until extinction, whatever the initial number of urediniospores and infectious branches.

Theorem 3.9. *If $\mathcal{R}_0^{(p)} < 1$, the DFE Q_p^0 of subsystems (3.1) is globally asymptotically stable (GAS).*

Proof. Consider the function

$$V_1 = a_1 L + b_1 I + c_1 J + d_1 U. \quad (3.13)$$

where a_1, b_1, c_1 and d_1 are positive constants to be chosen later. Consider then the following Lyapunov function candidate:

$$W_1 = \int_{\Omega} V_1 dx = \int_{\Omega} (a_1 L + b_1 I + c_1 J + d_1 U) dx, \quad (3.14)$$

where Ω is the spatial domain defined above.

Let us consider the set $\mathcal{V} = C\left((0, \infty); (\mathbf{L}^2(\Omega))^3 \times \mathbf{H}_{\eta}^2(\Omega)\right) \cap C\left([0, \infty); (\mathbf{L}^2(\Omega))^4\right) \cap C^1\left((0, \infty); (\mathbf{L}^2(\Omega))^4\right)$. For any solution $(L, I, J, U) \in \mathcal{V}$ of subsystems (3.1) with positive initial condition $(\phi_L(x), \dots, \phi_U(x))$, $W_1(L, \dots, U)$ is positive. Also, $W_1 = 0$ if and only if $(L, I, J, U) = (0, 0, 0, 0)$ on Ω .

The time derivative of the Lyapunov function W_1 along the trajectories of subsystems (3.1) satisfies:

$$\frac{dW_1}{dt} = \int_{\Omega} \dot{V}_1(L, I, J, U) dx. \quad (3.15)$$

From equation (3.13), one has that

$$\begin{aligned} \dot{V}_1 &= a_1 \frac{\partial L}{\partial t} + b_1 \frac{\partial I}{\partial t} + c_1 \frac{\partial J}{\partial t} + d_1 \frac{\partial U}{\partial t}, \\ &= a_1 \left(\frac{\omega_p \nu U}{N} S - (\theta_p + \mu_p) L \right) + b_1 (\theta_p L - (\alpha_p + \mu_p + d) I) + c_1 (\alpha_p I - \mu_M J) \\ &\quad + d_1 (\gamma_p I - (\nu + \mu_U) U) + d_1 \varepsilon \Delta U. \end{aligned} \quad (3.16)$$

Now, using the fact that $\frac{S}{N} \leq 1$, equation (3.16) becomes:

$$\dot{V}_1 \leq (-a_1(\theta_p + \mu_p) + b_1 \theta_p) L + (-b_1(\alpha_p + \mu_p + d) + c_1 \alpha_p + d_1 \gamma_p) I + (-d(\nu + \mu_U) + a_1 \omega_p \nu) U - c_1 \mu_p J + d_1 \varepsilon \Delta U. \quad (3.17)$$

Then, the positive constants a_1, b_1, c_1 and d_1 are chosen such that:

$$\begin{cases} -a_1(\theta_p + \mu_p) + b_1 \theta_p = 0, \\ -b_1(\alpha_p + \mu_p + d) + c_1 \alpha_p + d_1 \gamma_p = 0, \\ -d_1(\nu + \mu_U) + a_1 \omega_p \nu = 0. \end{cases} \quad (3.18)$$

Solving the above system (3.18) yields:

$$a_1 = \theta_p, \quad b_1 = \theta_p + \mu_p, \quad d_1 = \frac{\theta_p \omega_p \nu}{\nu + \mu_U} \quad \text{and} \quad c_1 = \frac{(\theta_p + \mu_p)(\alpha_p + \mu_p + d)}{\alpha_p} (1 - \mathcal{R}_0^{(p)}).$$

Note that $\mathcal{R}_0^{(p)} < 1$ ensures that $c_1 > 0$. Replacing the above expressions of a_1 , b_1 , c_1 and d_1 into equation (3.17), yields:

$$\dot{V}_1 \leq -c_1 \mu_p J + d_1 \varepsilon \Delta U. \quad (3.19)$$

Then equation (3.15) becomes:

$$\frac{dW_1}{dt} \leq - \int_{\Omega} c_1 \mu_p J dx + d_1 \varepsilon \int_{\Omega} \Delta U dx.$$

From the Neumann bounded condition $\frac{\partial U}{\partial \eta} = 0$, one has that:

$$\int_{\Omega} \Delta U dx = \int_{\partial \Omega} \frac{\partial U}{\partial \eta} = 0. \quad (3.20)$$

Thus, if $\mathcal{R}_0^{(p)} < 1$ one has:

$$\frac{dW_1}{dt} \leq - \int_{\Omega} c_1 \mu_p J dx. \quad (3.21)$$

Thus, $\mathcal{R}_0^{(p)} < 1$ ensures that $\frac{dW_1}{dt} \leq 0$ for all $L, I, J, U \geq 0$.

The domain $\Gamma_{\rho} = \{(L, I, J, U) \in \mathcal{V} : W_1(L, I, J, U) \leq \rho\}$, $\rho > 0$, is compact and includes the origin. Moreover, it is positively \mathcal{V} -invariant with respect the last four equations of subsystems (3.1). In fact, if the initial condition $(\phi_L, \phi_I, \phi_J, \phi_U) \in \Gamma_{\rho}$, we have

$$\frac{dW_1(L, I, J, U)}{dt} \leq 0 \Rightarrow W_1(L, I, J, U) \leq W_1(\phi_L, \phi_I, \phi_J, \phi_U) \leq \rho$$

Also, $\frac{dW_1}{dt} = 0$ if and only if $J = 0$, which from subsystems (3.1) is satisfied over a time interval of non-zero length only if $L = 0$, $I = 0$ and $U = 0$. Then it is easy to see that the largest invariant set defined over $\mathcal{E} = \{(L, I, J, U) \in \mathcal{V} : \frac{dW_1(L, I, J, U)}{dt} = 0\}$ is the singleton $\{(0, 0, 0, 0)\}$. Therefore, using LaSalle-Krasowski invariant principle [[14], Theorem 2] and the LAS in Lemma 3.8, one can conclude that $(L, I, J, U) = (0, 0, 0, 0)$ is GAS when $\mathcal{R}_0^{(p)} < 1$. Similar proofs adapting Lasalle's principle for PDE can be found in [35, 42].

Replacing of the value $U = 0$ into the first equation of subsystems (3.1) yields:

$$\dot{S} = \Lambda_p - \mu_p S. \quad (3.22)$$

The above equation (3.22) has a unique equilibrium $S_p^0 = \frac{\Lambda_p}{\mu_p}$, which is GAS. Hence, since the solutions of subsystems (3.1) are bounded, $S(x, t) \rightarrow S_p^0$. Thus, one can conclude that the DFE $Q_p^0 = (S_p^0, 0, 0, 0, 0)$ is globally asymptotically stable for subsystems (3.1). This concludes the proof. \square

3.3. Comparison of the dynamics in the dry and rainy seasons

The objective of this section is to compare the dynamics of subsystems (3.1) during the rainy and dry seasons. To this end, we first compare the basic reproduction numbers $\mathcal{R}_0^{(D)}$ and $\mathcal{R}_0^{(R)}$, and the number of infectious branches at the endemic equilibrium I_R^* and I_D^* . The former will indicate if and when CLR can persist within the coffee plantation, and the latter the intensity of the infection.

Simple biological hypotheses give the relation between the parameter values during the dry and rainy seasons. They mainly rely on the fact that some mechanisms require humid conditions: coffee tree growth is faster during

the rainy season ($\Lambda_D \leq \Lambda_R$), germination occurs mostly during the rainy season ($\omega_D \leq \omega_R$), the lesion progresses faster during the rainy season ($\theta_D \leq \theta_R$) and the mortality rate of the branches is higher during the dry season (as a consequence of harvest, which always damages some branches) i.e ($\mu_R \leq \mu_D$). Hence, we have:

$$\Lambda_D \leq \Lambda_R, \quad \omega_D \leq \omega_R, \quad \theta_D \leq \theta_R, \quad \mu_R \leq \mu_D, \quad \gamma_D = \gamma_R \quad \text{and} \quad \alpha_D = \alpha_R. \quad (3.23)$$

3.3.1. Comparison of the basic reproduction numbers

Herein we compare the basic reproduction numbers of the subsystems:

$$\mathcal{R}_0^{(R)} = \frac{\gamma_R}{(\nu + \mu_U)} \frac{\nu \theta_R \omega_R}{(\theta_R + \mu_R)(\alpha_R + \mu_R + d)} \quad \text{and} \quad \mathcal{R}_0^{(D)} = \frac{\gamma_D}{(\nu + \mu_U)} \frac{\nu \theta_D \omega_D}{(\theta_D + \mu_D)(\alpha_D + \mu_D + d)}.$$

Using (3.23), one has:

$$\mathcal{R}_0^{(D)} \leq \mathcal{R}_0^{(R)}. \quad (3.24)$$

This means that the GAS of the DFE Q_R^0 during the rainy season implies the GAS of the DFE Q_D^0 during the dry season and the existence and local asymptotic stability of the endemic equilibrium Q_D^* during the dry season implies the existence and local asymptotic stability of the endemic equilibrium Q_R^* during the rainy season. Biologically speaking, if the disease is present during the dry season, it will be also present during the rainy season while, if the disease is absent during the rainy season, it will be also absent during the dry season.

3.3.2. Comparison of the infectious branches at the endemic level

To compare the disease at the endemic level, both basic reproduction numbers need to be greater than one, $1 < \mathcal{R}_0^{(p)}$ for $p = D$ and R . The expression of I_p^* depends on the parameters identified in (3.23). The partial derivatives of I_p^* with respect to parameters Λ_p , ω_p , θ_p and μ_p are:

$$\begin{aligned} \frac{\partial I_p^*}{\partial \Lambda_p} &= \frac{(\nu + \mu_U)(\mathcal{R}_0^{(p)} - 1)}{\gamma_p \omega_p \nu - d(\nu + \mu_U)} > 0, & \frac{\partial I_p^*}{\partial \omega_p} &= \frac{\gamma_p \nu (\theta_p (\alpha_p + \mu_p) + \mu_p (\alpha_p + \mu_p + d))}{[\gamma_p \omega_p \nu - d(\nu + \mu_U)](\theta_p + \mu_p)(\alpha_p + \mu_p + d)} > 0, \\ \frac{\partial I_p^*}{\partial \theta_p} &= \frac{\gamma_p \nu \omega_p \mu_p}{(\omega_p + \mu_p)} > 0, & \frac{\partial I_p^*}{\partial \mu_p} &= -\frac{\gamma_p \nu \omega_p \theta_p (\theta_p + 2\mu_p + \alpha_p d)}{[\gamma_p \omega_p \nu - d(\nu + \mu_U)](\theta_p + \mu_p)(\alpha_p + \mu_p + d)} < 0. \end{aligned}$$

This shows that I_p^* is an increasing function if Λ_p , ω_p , θ_p and a decreasing function of μ_p . Now, using (3.23), we can deduce that:

$$I_R^* > I_D^*. \quad (3.25)$$

Therefore, if it reached equilibrium, the CLR would be more severe during the rainy season than during the dry season.

4. NUMERICAL SIMULATIONS

Herein, we present the results of numerical simulations of system (2.1) using a non standard finite difference method [23]. We take $T = 365$ days and $\tau = 120$ days which correspond to the durations of the year and the dry season in Cameroon, respectively. We set $\Omega = [0, 100]$ meters. We consider that initially all branches are healthy, that urediniospores are concentrated in the middle of the plantation and that there are no berries, so

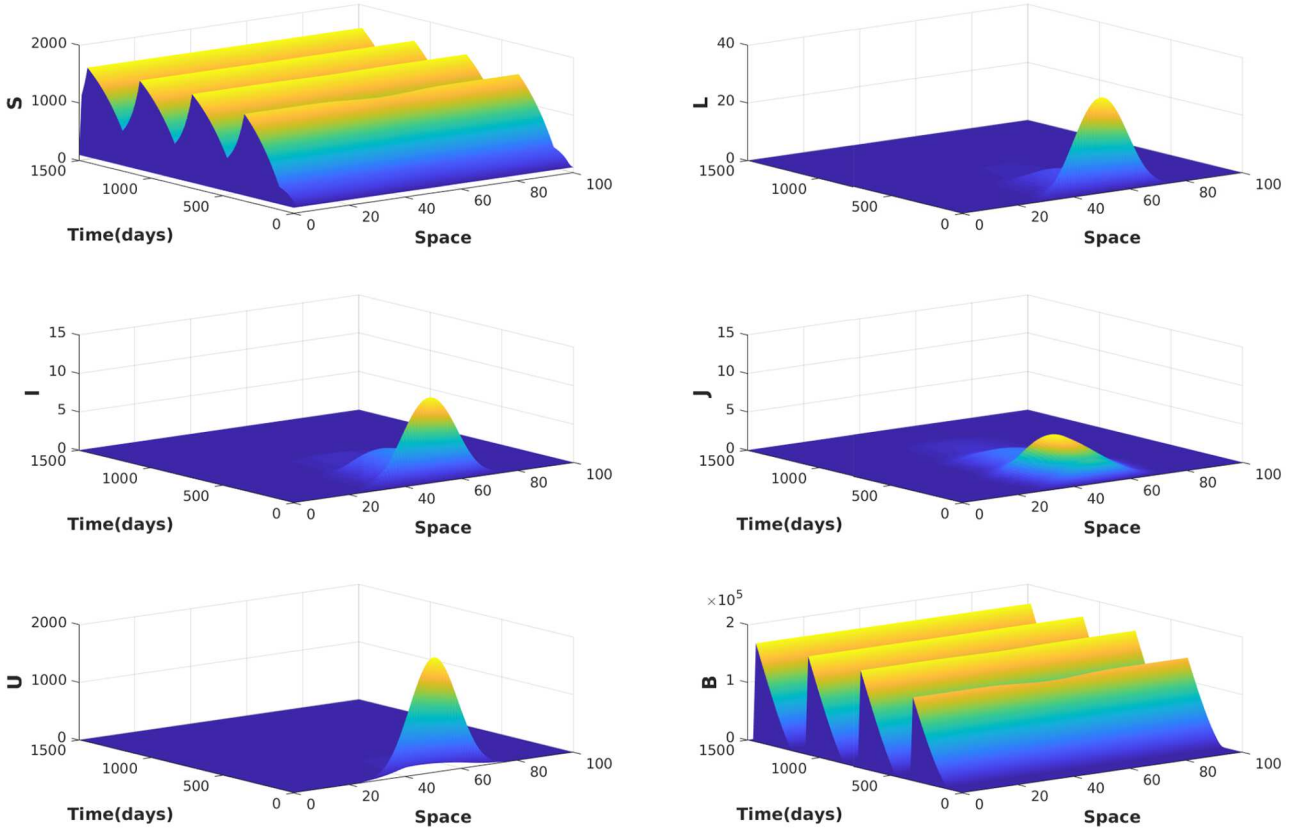


FIGURE 2. Spatio-temporal simulation of system (2.1), (2.4), (4.1) when $\gamma_D = \gamma_R = 1.5$, which leads to $\mathcal{R}_0^{(D)} = 0.52$ and $\mathcal{R}_0^{(R)} = 0.95$. All other parameter values are given in Table 1. Subplots represent healthy branches S , latent branches L , infectious branches I , leafless branches J , urediniospores U and berries B .

the initial conditions are, $\forall x \in \Omega$:

$$\begin{cases} S_0(x) = 100, & L_0(x) = I_0(x) = J_0(x) = 0, \\ U_0(x) = 2000 \sin^{14}\left(\frac{\pi x}{100}\right) \\ B_0(x) = 0. \end{cases} \quad (4.1)$$

Table 1 summarizes the parameter values for system (2.1) used for numerical simulations. We suppose that γ_p and α_p have the same value during the dry and rainy seasons.

4.1. CLR dynamics

We first choose $\gamma_p = 1.5$ for $p = D$ and R , so that $\mathcal{R}_0^{(D)} = 0.52$ and $\mathcal{R}_0^{(R)} = 0.95$. Figure 2 presents the spatio-temporal evolution of system (2.1) with these parameters in domain Ω during time interval $[0, 1500]$ days. Urediniospores are initially present in the middle of the Ω interval, which induces local CLR infection during the first year. Subsequently, the infection dies out, as L , I , J and U go to 0. The S and B variables regain their healthy levels, corresponding to the stationary periodic disease-free solution. This illustrates Theorem 3.9: since $\mathcal{R}_0^{(D)}$ and $\mathcal{R}_0^{(R)}$ are smaller than one, the disease should vanish during both the dry and rainy seasons; we see here that connecting both seasons preserves this property.

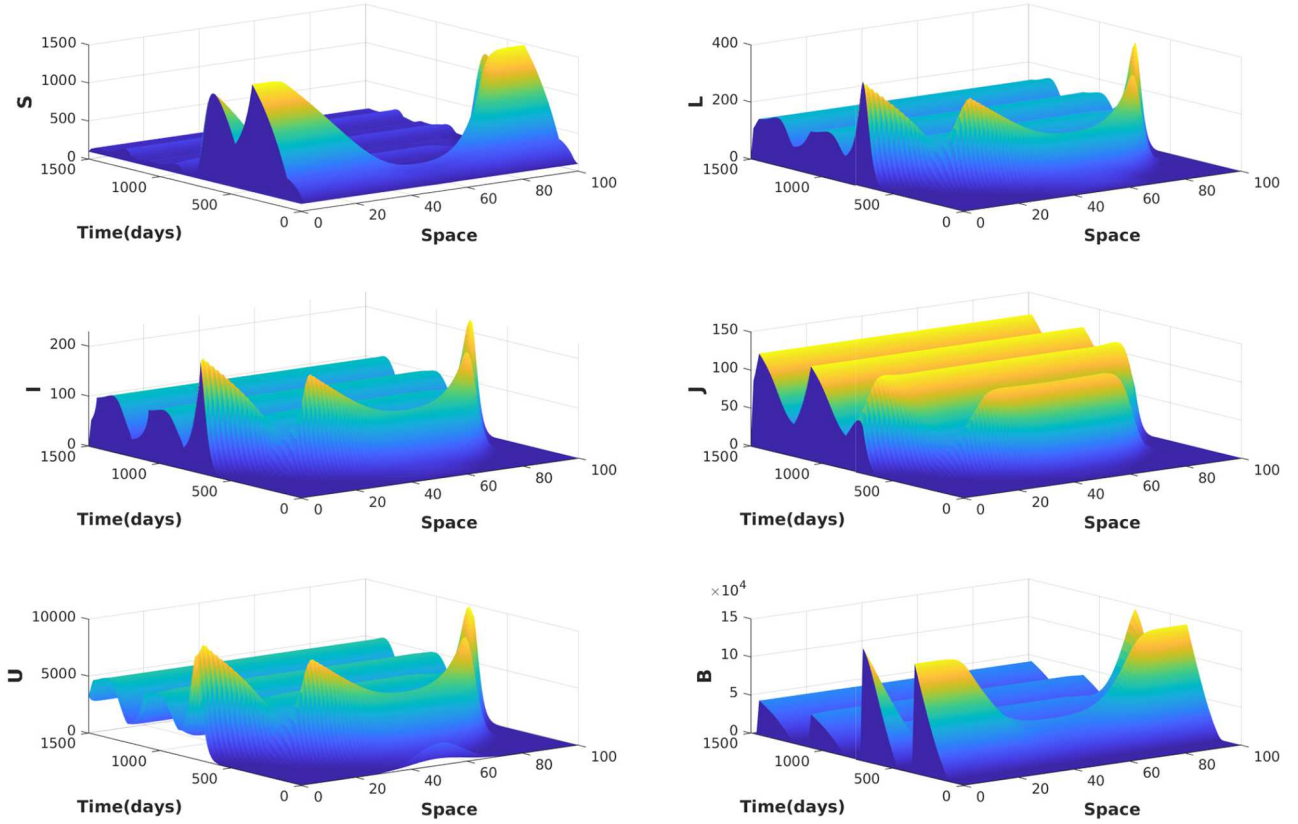


FIGURE 3. Spatio-temporal simulation of system (2.1,2.4,4.1) when $\gamma_D = \gamma_R = 8$, which leads to $\mathcal{R}_0^{(R)} = 5.09$ and $\mathcal{R}_0^{(D)} = 2.77$. All other parameter values are given in Table 1. Subplots represent healthy branches S , latent branches L , infectious branches I , leafless branches J , urediniospores U and berries B .

Then we choose $\gamma_p = 8$ for $p = D$ and R , so that $\mathcal{R}_0^{(R)} = 5.09$ and $\mathcal{R}_0^{(D)} = 2.77$. In this case, we have shown in Lemma 3.8 that the endemic equilibria exist and is locally asymptotically stable during both seasons. Numerical results are shown in Figure 3. One can observe that the peaks of the infectious branches and urediniospores flatten very quickly compared to the other variables. The convergence towards the endemic stationary solution is clear at the beginning of the third year (after 1000 days approximately). Oscillations are observed, as the endemic equilibrium is higher during the rainy season (subsystem (3.1) with $p = R$) than the dry season (subsystem (3.1) with $p = D$). Note that urediniospores hardly reach the edges of the plantation during the first year, so that healthy branches are produced in large quantity, contrary to the middle of the plantation where urediniospores directly infect branches, which limits growth. Hence, when the urediniospores reach the edges during the second year, there is a large infection peak at the edges, which contrasts with the middle of the plantation.

Figure 4 is a temporal representation of Figure 3 for three different values of x taken in the centre of the domain ($x = 50$ m, yellow curve), on the border ($x = 1$ m, blue curve) and in-between ($x = 25$ m, red curve). Convergence towards the stationary endemic solution can also be observed here, as all curves overlap for the three x values at the end of the third year and on. At the centre of the domain, the system very rapidly converges towards this stationary solution, but it takes a year for $x = 25$ m. On the border of the domain, branches remain susceptible during almost two years. Then the number of latent L and infectious I branches peak, as urediniospores U , initially in the centre of the domain, reach its borders. These peaks occur during the

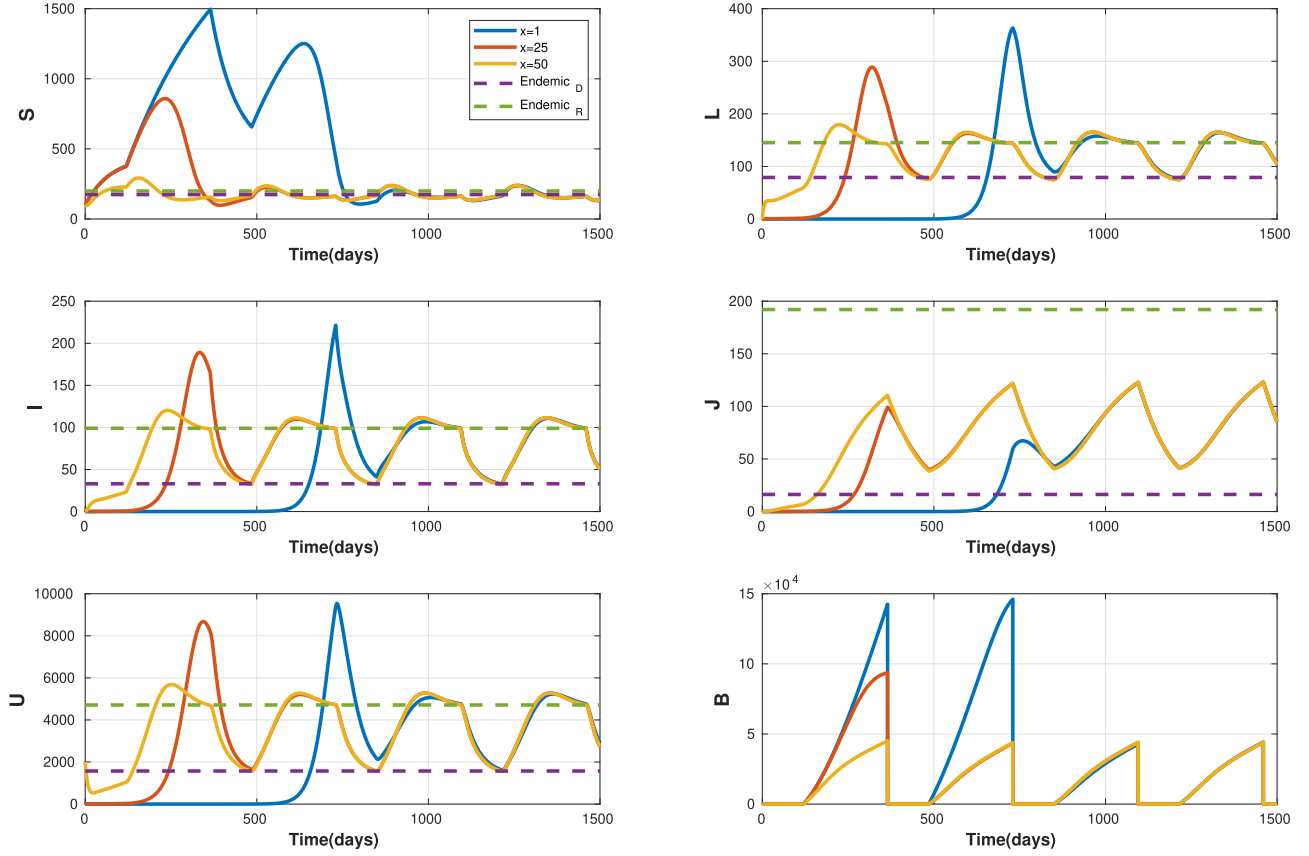


FIGURE 4. Temporal simulation, for three values of x , of system (2.1, 2.4, 4.1) when $\gamma_D = \gamma_R = 8$, which leads to $\mathcal{R}_0^{(R)} = 5.09$ and $\mathcal{R}_0^{(D)} = 2.77$ (as in Fig. 3). All other parameter values are given in Table 1. x is chosen in the centre of the domain (yellow curve), on the border (blue curve) and in-between (red curve). Subplots represent healthy branches S , latent branches L , infectious branches I , leafless branches J , urediniospores U and berries B .

second rainy season. However, no such peak is observed for leafless branches J . Indeed, the number of leafless branches starts to increase at the end of the second rainy season (around time $t = 600$ days), but the arrival of the dry season reduces the number of branches before it can peak very high. Solutions then oscillate between the endemic equilibria of the dry and rainy seasons (purple and green dashed lines, respectively). Infection has a negative impact on the production, which is reduced to less than a third of its value without disease.

These simulations allow to conclude that the dynamics of system (2.1), can be inferred from the dynamics of subsystems (3.1) during the dry and rainy seasons.

4.2. Control of CLR

Integrated pest management currently used for the control of CLR [1] relies on the following methods:

- cultural practices, including stumping of diseased plants, shading, spore traps [2];
- chemical control by copper, triazole or dithiocarbamate fungicides [10];
- genetic control based on wild rust-resistant *Coffea* species [2];

- biological control based on *Hemileia vastatrix* natural enemies, *e.g.* mycoparasites such as *Lecanicillium lecanii* [11, 39], or antagonistic bacteria such as *Pseudomonas putida* P286 and *Bacillus thuringiensis* B157 [16, 17]; it can also rely on natural allies of the crop such as benefic endophytes [32, 33].

Biological control is a potentially powerful tool for managing coffee leaf rust that allows organic certification. Therefore, we introduced in this study a mycoparasite (a parasitic fungus whose host is another fungus), *Lecanicillium lecanii*, known to hamper the reproduction of *H. vastatrix*. In our model, this biocontrol agent reduces the production of urediniospores by infectious branches with an efficiency q . The production rate of urediniospores γ_p hence becomes $(1 - q)\gamma_p$ and system (3.1) becomes:

$$\begin{cases} \partial_t S = \Lambda_p - \frac{\omega_p \nu U}{N} S - \mu_p S, \\ \partial_t L = \frac{\omega_p \nu U}{N} S - (\theta_p + \mu_p) L, \\ \partial_t I = \theta_p L - (\alpha_p + \mu_p + d) I, \\ \partial_t J = \alpha_p I - \mu_p J, \\ \partial_t U = \varepsilon \Delta U + (1 - q)\gamma_p I - (\nu + \mu_U) U. \end{cases} \quad (4.2)$$

The basic reproduction numbers of system (4.2), for $p = D$ and R , are then:

$$\mathcal{R}_0^{(p)} = \frac{(1 - q)\gamma_p \nu}{(\nu + \mu_U)} \frac{\theta_p \omega_p}{(\theta_p + \mu_p)(\alpha_p + \mu_p + d)}. \quad (4.3)$$

The higher the biocontrol efficiency q , the lower the reproduction numbers. So high enough values of q should allow to control the disease.

We simulated system (4.2) for different values of biocontrol efficiency q over 8 years. Figure 5 presents the temporal evolution of the state variables (S, L, I, J, U, B) integrated over domain Ω . Table 2 provides the reproduction numbers defined in equation (4.3), as well as the berry production and production loss during the 8th year, the latter being computed by reference to the disease-free case $q = 1$.

- $q = 0$ corresponds to no control (red curves) and $\mathcal{R}_0^{(R)} > \mathcal{R}_0^{(D)} > 1$, as in previous Section 4.1. The yield loss is as high as 80.1%.
- For a 50% efficiency (cyan curves), which still corresponds to $\mathcal{R}_0^{(R)} > \mathcal{R}_0^{(D)} > 1$, the number of spores U drops as expected, as the mycoparasite hampers the production of spores. So the number of healthy branches S increases. However, the number of latent L , infectious I and leafless J branches, barely change. Indeed, the production of latent branches depends on the product SU . The production of berries B then increases, as it is mostly driven by the healthy branches, but the yield loss is still high at 68.2%.
- For a 70% efficiency (magenta curves), corresponding to $\mathcal{R}_0^{(R)} > 1 > \mathcal{R}_0^{(D)}$, these observations are amplified: spores seriously drop; healthy branches and berries largely increase; latent, infectious and leafless branches decrease. The yield loss is 33.5%.
- For a 75% efficiency (black curves), also corresponding to $\mathcal{R}_0^{(R)} > 1 > \mathcal{R}_0^{(D)}$, infection remains very low, leading to an acceptable 6.0% yield loss.
- An 76% efficiency (blue curves), still corresponding to $\mathcal{R}_0^{(R)} > 1 > \mathcal{R}_0^{(D)}$, almost yields the same results as a perfect efficiency ($q = 1$). Infection is almost negligible, so the yield loss is as low as 1.8%.
- $q = 1$ (green curves) corresponds to a perfect (and unrealistic) efficiency, with $\mathcal{R}_0^{(R)} = \mathcal{R}_0^{(D)} = 0$, leading to the disease extinction and no yield loss.

Hence a 75% biocontrol efficiency is enough to sustain the berry production in the plantation, with a negligible yield loss. Higher efficiencies, moreover, achieve disease eradication.

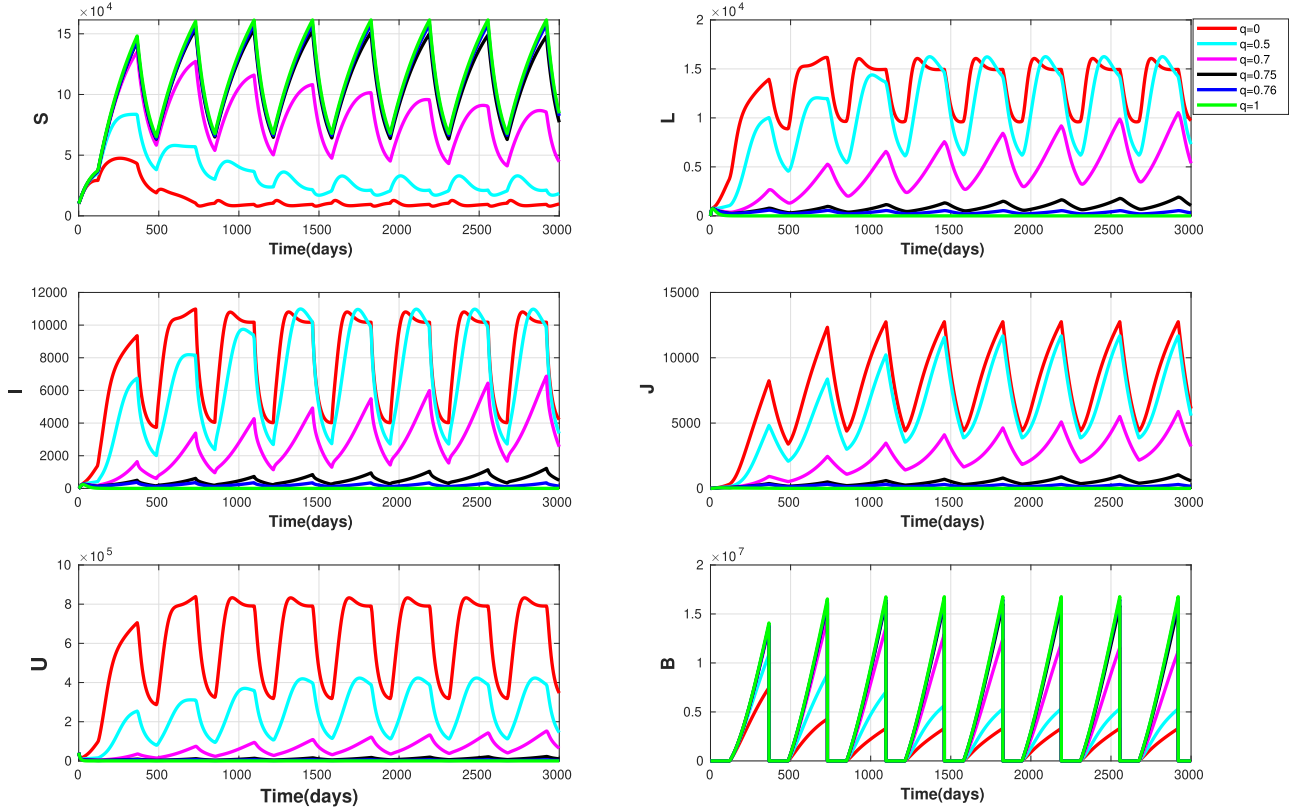


FIGURE 5. Temporal simulations, for various efficiencies q of the biocontrol mycoparasite, of controlled system (4.2,2.4,4.1) when $\gamma_D = \gamma_R = 8$. All other parameter values are given in Table 1. Subplots represent healthy branches S , latent branches L , infectious branches I , leafless branches J , urediniospores U and berries B , these variables being integrated over domain Ω .

TABLE 2. Impact of biocontrol efficiency q on reproduction numbers, defined in (4.3), and on berry production during the 8th and last year.

Biocontrol efficiency	$q = 0$	$q = 0.5$	$q = 0.7$	$q = 0.75$	$q = 0.76$	$q = 1$
$\mathcal{R}_0^{(D)}$	2.77	1.38	0.83	0.69	0.66	0
$\mathcal{R}_0^{(R)}$	5.09	2.54	1.52	1.27	1.22	0
Number of berries	33.2×10^5	53.1×10^5	111×10^5	157×10^5	164×10^5	167×10^5
Yield loss (%)	80.1	68.2	33.5	6.0	1.8	0

5. CONCLUSION

In this paper, we have proposed and analysed a PDE model that describes the dispersal of CLR in a coffee plantation during the rainy and dry seasons and its behaviour over time. Furthermore, we computed the disease-free and endemic equilibria of the two subsystems defined during the rainy and dry seasons. We showed that the basic reproduction numbers during the two seasons can determine the dynamics of global model: when the basic reproduction number is less than one during the rainy season, then CLR globally decreases till extinction; when it is greater than one for the dry season, then CLR persists.

We implemented a biocontrol in our model, corresponding to a mycoparasite such as *Lecanicillium lecanii*, which hampers CLR reproduction at all times. This solution was tested in Mexico [11] but is still under

development. A rather high biocontrol efficiency (75% at least) is necessary in our model to control the disease, but lower efficiencies still improve coffee production notably. Moreover, the mycoparasite is applied all year round, so it is not easily implemented in practice and it involves important costs. It would be interesting to study when to deploy the mycoparasite in a cost-efficient way. An ideal mycoparasite should sustain the dry season and efficiently control CLR, so that the coffee plantation during the rainy season would suffer reasonable yield losses. In further work, we will also include cultural management and other biocontrol agents, in particular natural endophytes which are affordable for growers starting a new plantation.

Several extensions to this work are considered: (i) adding a stage structure on the coffee branches; (ii) simplifying the model, using an impulsive formalism for the dry season as in [22, 45], in order to obtain analytical results on the global model behaviour; (iii) solving an optimal control problem, consisting in maximising coffee production while minimising the control costs.

APPENDIX A.

Proof of Lemma 3.8.

– *Local stability of the disease-free equilibrium*

Let (S, L, I, J, U) be a solution of subsystems (3.1). Then, according to Kiehöfer [20], this solution can be written in the following form:

$$(S, L, I, R, U) = Q_p^0 + (W_1, W_2, W_3, W_4, W_5), \quad x \in \Omega, \quad t > 0. \quad (\text{A.1})$$

With this in mind, subsystems (3.1) can be written in the following compact form:

$$\frac{\partial W}{\partial t} = \mathcal{D}\Delta W + F(W), \quad (\text{A.2})$$

where $\mathcal{D} = \text{diag}(0, 0, 0, 0, 0, \varepsilon)$. The linearisation of subsystems (A.2) in the neighbourhood of Q_p^0 is:

$$\frac{\partial W}{\partial t} = \mathcal{D}\Delta W + L(Q_p^0)W, \quad (\text{A.3})$$

where $L(Q_p^0)$ is the Jacobian matrix at the DFE Q_p^0 of subsystems (3.1) in the absence of diffusion, that is:

$$L(Q_p^0) = \begin{pmatrix} -\mu_p & 0 & 0 & 0 & -\omega_p\nu \\ 0 & -(\theta_p + \mu_p) & 0 & 0 & \omega_p\nu \\ 0 & \theta_p & -(\alpha_p + \mu_p + d) & 0 & 0 \\ 0 & 0 & \alpha_p & -\mu_p & 0 \\ 0 & 0 & \gamma_p & 0 & -(\nu + \mu_U) \end{pmatrix}.$$

Let g_j , $j \in \mathbb{N}$, be the j^{th} eigenfunction of operator $-\Delta$ with Neumann boundary conditions, so that:

$$\begin{cases} -\Delta g_j = \lambda_j g_j & \text{in } \Omega, \\ \frac{\partial g_j}{\partial \eta} \big|_{\partial\Omega} = 0 & \text{on } \partial\Omega, \end{cases} \quad (\text{A.4})$$

where λ_j are the associated eigenvalues verifying $0 = \lambda_0 < \lambda_1 < \lambda_2 < \dots$

According to [20], the expanded expression of W in equation (A.3) can be written as:

$$W = \sum_{j=0}^{\infty} Y_j(t) g_j(x),$$

where each $Y_j(t) \in \mathbb{R}^5$. Substituting this expression into equation (A.3) yields:

$$\frac{dY_j}{dt} = (L(Q_p^0) - \lambda_j \mathcal{D}) Y_j. \quad (\text{A.5})$$

Thus, the DFE Q_p^0 is stable if and only if each $Y_j(t) \rightarrow 0$ when $t \rightarrow \infty$, that is, if and only if all the eigenvalues of matrix $H_j = L(Q_p^0) - \lambda_j \mathcal{D}$ have negative real parts. Matrix H_j can be written in the following form:

$$H_j = \begin{pmatrix} -\mu_p & 0 & 0 & 0 & -\omega_p \nu \\ 0 & -(\theta_p + \mu_p) & 0 & 0 & \omega_p \nu \\ 0 & \theta_p & -(\alpha_p + \mu_p + d) & 0 & 0 \\ 0 & 0 & \alpha_p & -\mu_p & 0 \\ 0 & 0 & \gamma_p & 0 & -(\nu + \mu_U + \varepsilon \lambda_j) \end{pmatrix}.$$

The characteristic polynomial of matrix H_j is given by

$$P_1(X) = (X + \mu_p)^2 (X^3 + a_2 X^2 + a_1 X + a_0)$$

where

$$\begin{cases} a_2 = \theta_p + 2\mu_p + \alpha_p + d + \nu + \mu_U + \varepsilon \lambda_j \\ a_1 = (\theta_p + \mu_p)(\alpha_p + \mu_p + d + \nu + \mu_U + \varepsilon \lambda_j) + (\alpha_p + \mu_p + d)(\nu + \mu_U + \varepsilon \lambda_j) \\ a_0 = (\theta_p + \mu_p)(\alpha_p + \mu_p + d)(\nu + \mu_U + \varepsilon \lambda_j) - \gamma_p \theta_p \omega_p \nu \end{cases}$$

Firstly one can observe that $a_2 > 0$, $a_1 > 0$ and

$$a_0 = (\theta_p + \mu_p)(\alpha_p + \mu_p + d)(\nu + \mu_U + \varepsilon \lambda_j) \left(1 - \frac{\gamma_p \theta_p \omega_p \nu}{(\theta_p + \mu_p)(\alpha_p + \mu_p + d)(\nu + \mu_U + \varepsilon \lambda_j)} \right)$$

Hence $a_0 > 0$ if $\frac{\gamma_p \theta_p \omega_p \nu}{(\theta_p + \mu_p)(\alpha_p + \mu_p + d)(\nu + \mu_U + \varepsilon \lambda_j)} < 1$, which is satisfied for all (non negative) λ_j if it is satisfied for $\lambda_0 = 0$. The condition $a_0 > 0$ then leads to:

$$\mathcal{R}_0^{(p)} = \frac{\gamma_p \theta_p \omega_p \nu}{(\theta_p + \mu_p)(\alpha_p + \mu_p + d)(\nu + \mu_U)} < 1. \quad (\text{A.6})$$

Secondly, the expression

$$\begin{aligned} a_2 a_1 - a_0 &= (\alpha_p + \mu_p + d + \nu + \mu_U + \varepsilon \lambda_j)(\theta_p + \mu_p)^2 + (\theta_p + \mu_p)(\alpha_p + \mu_p + d + \nu + \mu_U + \varepsilon \lambda_j) \\ &\quad + (\alpha_p + \mu_p + d)(\nu + \mu_U + \varepsilon \lambda_j) + \gamma_p \theta_p \omega_p \nu > 0 \end{aligned}$$

Using the fact that $a_2 > 0$, $a_1 > 0$, $a_0 > 0$ and $a_2 a_1 > a_0$, the Routh–Hurwitz stability criterion indicates that all the eigenvalues of matrix H_j have negative real parts. Hence the DFE Q_p^0 of subsystems (3.1) is LAS if and only if $\mathcal{R}_0^{(p)} < 1$.

- *Existence and local stability of the endemic equilibrium Q_p^**

Suppose that $\mathcal{R}_0^{(p)} > 1$. The expression (3.12) of the endemic equilibrium can easily be established as the solution of a set of linear equations, derived from equating the right-hand side of equation (3.1) to zero. We first prove that I_p^* and S_p^* are positive. Recall that:

$$I_p^* = \frac{\Lambda_p(\nu + \mu_U)(\mathcal{R}_0^{(p)} - 1)}{\gamma_p \omega_p \nu - d(\nu + \mu_U)} \quad \text{and} \quad S_p^* = \frac{\Lambda_p(\gamma_p \omega_p \nu - d(\nu + \mu_U)\mathcal{R}_0^{(p)})}{\mu_p \mathcal{R}_0^{(p)}(\gamma_p \omega_p \nu - d(\nu + \mu_U))}.$$

Note that:

$$\begin{aligned} \mathcal{R}_0^{(p)} > 1 &\Rightarrow \frac{\gamma_p \omega_p \nu \theta_p}{(\nu + \mu_U)(\theta_p + \mu_p)(\alpha + \mu_p + d)} > 1, \\ &\Rightarrow d < \frac{\gamma_p \omega_p \nu \theta_p}{(\nu + \mu_U)(\theta_p + \mu_p)} - \alpha_p - \mu_p, \\ &\Rightarrow d < \frac{\gamma_p \omega_p \nu \theta_p}{(\nu + \mu_U)(\theta_p + \mu_p)}, \\ &\Rightarrow d(\nu + \mu_U) < \frac{\gamma_p \omega_p \nu \theta_p}{(\theta_p + \mu_p)} < \gamma_p \omega_p \nu \\ &\Rightarrow \gamma_p \omega_p \nu - d(\nu + \mu_U) > 0, \\ &\Rightarrow I_p^* > 0. \end{aligned}$$

Now using the fact that $\frac{\theta_p d}{(\theta_p + \mu_p)(\alpha_p + \mu_p + d)} < 1$, one has:

$$\begin{aligned} \frac{\gamma_p \omega_p \nu \theta_p d(\nu + \mu_U)}{(\nu + \mu_U)(\theta_p + \mu_p)(\alpha_p + \mu_p + d)} &< \gamma_p \omega_p \nu \Rightarrow (\nu + \mu_U)\mathcal{R}_0^{(p)} < \gamma_p \omega_p \nu, \\ &\Rightarrow \gamma_p \omega_p \nu - d(\nu + \mu_U)\mathcal{R}_0^{(p)} > 0 \\ &\Rightarrow S_p^* > 0 \end{aligned}$$

This concludes the existence of the endemic equilibrium.

Second, we investigate the local stability of the endemic equilibrium, using the following theorem.

Theorem A.1 (Castillo-Chavez and Song [12]). *Consider the following ordinary differential equations, with a parameter ψ :*

$$\frac{dx}{dt} = f(x, \psi), \quad f : \mathbb{R}^n \times \mathbb{R}^n \mathbb{R}^n \quad \text{and} \quad f \in C^2(\mathbb{R}^n \times \mathbb{R}). \quad (\text{A.7})$$

Without loss of generality, it is assumed that 0 is an equilibrium for system (A.7) for all values of the parameter ψ , that is $f(0, \psi) \equiv 0$ for all ψ . Assume

- A_1 : $A = D_x f(0, 0) = (\frac{\partial f_i}{\partial x_j}(0, 0))$ is the linearization matrix of system (A.7) around the equilibrium 0 with ψ evaluated at 0. Zero is a simple eigenvalue of A and all other eigenvalues of A have negative real parts;
 A_2 : Matrix A has a nonnegative right eigenvector u and a left eigenvector v corresponding to the zero eigenvalue. Let f_k be the k^{th} component of f and

$$a = \sum_{k,i,j=1}^n v_k u_i u_j \frac{\partial^2 f_k}{\partial z_i \partial z_j}(0, 0), \quad \text{and} \quad b = \sum_{k,i=1}^n v_k u_i \frac{\partial^2 f_k}{\partial z_i \partial \psi}(0, 0).$$

The local dynamics of (A.7) around 0 are totally determined by a and b .

- $a > 0, b > 0$. When $\psi < 0$ with $\|\psi\| \ll 1$, 0 is locally asymptotically stable, and there exists a positive unstable equilibrium; when $0 < \psi \ll 1$, 0 is unstable and there exists a negative and locally asymptotically stable equilibrium;
- $a < 0, b < 0$. When $\psi < 0$ with $\|\psi\| \ll 1$, 0 is unstable; when $0 < \psi \ll 1$, 0 is locally asymptotically stable, and there exists a positive unstable equilibrium;
- $a > 0, b < 0$. When $\psi < 0$ with $\|\psi\| \ll 1$, 0 is unstable, and there exists a locally asymptotically stable negative equilibrium; when $0 < \psi \ll 1$, 0 is stable, and a positive unstable equilibrium appears;
- $a < 0, b > 0$. When ψ changes from negative to positive, 0 changes its stability from stable to unstable. Correspondingly a negative unstable equilibrium becomes positive and locally asymptotically stable.

In order to apply this theorem, subsystems (3.1) can be written as follows, with $z = (S, L, I, J, U)$:

$$\begin{cases} \frac{\partial_t z_1}{\partial t} = F_1 = \Lambda_p - \mu_p z_1 - \frac{\omega_p \nu z_5}{z_1 + z_2 + z_3 + z_4}, \\ \frac{\partial_t z_2}{\partial t} = F_2 = \frac{\omega_p \nu z_5}{z_1 + z_2 + z_3 + z_4} - (\theta_p + \mu_p) z_2, \\ \frac{\partial_t z_3}{\partial t} = F_3 = \theta_p z_2 - (\alpha + \mu_p + d) z_3, \\ \frac{\partial_t z_4}{\partial t} = F_4 = \alpha_p z_3 - \mu_p z_4, \\ \frac{\partial_t z_5}{\partial t} - \varepsilon \Delta z_5 = F_5 = \gamma_p z_3 - (\nu + \mu_U) z_5, \end{cases} \quad (\text{A.8})$$

Solving $\mathcal{R}_0^{(p)} = 1$, we obtain the following bifurcation value for parameter ω_p :

$$\omega_p^* = \frac{(\mu_p + \theta)(\alpha_p + \mu_p + d)(\nu + \mu_U)}{\nu \gamma_p \theta_p}.$$

We linearise this system at the DFE Q_p^0 , as previously in equation (A.5), setting ω_p to ω_p^* . We need to determine the eigenvalues of matrix $L_{\omega_p^*} - \lambda_j \mathcal{D}$, where λ_j is an eigenvalue of the Laplacian operator $-\Delta$ (simplified notation $L_{\omega_p^*}$ is used instead of $L_{\omega_p^*}(Q_p^0)$). With $\lambda_j = \lambda_0 = 0$, the matrix admits $\beta_0 = 0$ as eigenvalue, the other eigenvalues still having a negative real part. For the other λ_j , all eigenvalues have negative real parts. So assumption A_1 of theorem A.1 is verified.

Let us now verify assumption A_2 . We need to compute the left and right eigenvectors of matrix $L_{\omega_p^*} - \lambda_j \mathcal{D}$ associated with the eigenvalue β . The left eigenvector, denoted by $v = (v_1, v_2, v_3, v_4, v_5)$, satisfies the following equation:

$$v(L_{\omega_p^*} - \lambda_j \mathcal{D} - \beta \mathbf{I}) = \mathbf{0},$$

where \mathbf{I} and $\mathbf{0}$ are the identity matrix and null vector of dimension 5, respectively. For $\beta = \beta_0 = 0$ one has:

$$(v_1 \ v_2 \ v_3 \ v_4 \ v_5) \begin{pmatrix} -\mu_p & 0 & 0 & 0 & -\omega_p^* \nu \\ 0 & -(\theta_p + \mu_p) & 0 & 0 & \omega_p^* \nu \\ 0 & \theta_p & -(\alpha_p + \mu_p + d) & 0 & 0 \\ 0 & 0 & \alpha_p & -\mu_p & 0 \\ 0 & 0 & \gamma_p & 0 & -(\nu + \mu_U + \varepsilon \lambda_j) \end{pmatrix} = (0 \ 0 \ 0 \ 0 \ 0)$$

which gives:

$$\begin{cases} v_1 = 0, \\ v_2 = \frac{\gamma_p \theta_p}{(\mu_p + \theta_p)(\alpha_p + \mu_p + d)} v_5, \\ v_3 = \frac{\gamma_p}{(\alpha_p + \mu_p + d)} v_5, \\ v_4 = 0, \\ v_5 > 0. \end{cases}$$

Similarly the right eigenvector of matrix $L_{\omega_p^*} - \lambda_j \mathcal{D}$, denoted by $u = (u_1, u_2, u_3, u_4, u_5)^T$, satisfies the following equation:

$$(L_{\omega_p^*} - \lambda_j \mathcal{D} - \beta \mathbf{I})u = \mathbf{0}.$$

For $\beta = \beta_0 = 0$, one has:

$$\begin{pmatrix} -\mu_p & 0 & 0 & 0 & -\omega_p^* \nu \\ 0 & -(\theta_p + \mu_p) & 0 & 0 & \omega_p^* \nu \\ 0 & \theta_p & -(\alpha_p + \mu_p + d) & 0 & 0 \\ 0 & 0 & \alpha_p & -\mu_p & 0 \\ 0 & 0 & \gamma_p & 0 & -(\nu + \mu_U + \varepsilon \lambda_j) \end{pmatrix} \begin{pmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \\ u_5 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix},$$

which gives:

$$\begin{cases} u_1 = -\frac{\omega_p^* \nu}{\mu} u_5, \\ u_2 = \frac{\omega_p^* \nu}{\mu + \theta} u_5, \\ u_3 = \frac{\omega_p^* \nu \theta}{(\mu + \theta)(\alpha_p + \mu_p + d)} u_5, \\ u_4 = \frac{\alpha_p \omega_p^* \nu \theta_p}{(\mu_p + \theta_p)(\alpha_p + \mu_p + d)} u_5, \\ u_5 > 0. \end{cases}$$

Let us now compute a , defined in assumption A_2 of theorem A.1, for system (A.8):

$$a = \sum_{i,j,k=1}^5 v_k u_i u_j \frac{\partial^2 F_k}{\partial z_i \partial z_j} (Q_p^0, \omega_p^*).$$

The only terms that are non null correspond to:

$$\frac{\partial^2 F_2}{\partial z_i \partial z_5} (Q_p^0, \omega_p^*) = v_2 \frac{\partial^2 F_2}{\partial z_5 \partial z_j} (Q_p^0, \omega_p^*) = -\frac{\omega_p \nu^*}{S^0} \quad \text{for } i, j = 2, 3, 4.$$

Substituting these terms into the expression of a , one obtains:

$$\begin{aligned} a &= v_2 \left[2u_2u_5 \frac{\partial^2 F_2}{\partial z_2 \partial z_5}(Q_p^0, \omega_p^*) + 2u_3u_5 \frac{\partial^2 F_2}{\partial z_3 \partial z_5}(Q_p^0, \omega_p^*) + 2u_4u_5 \frac{\partial^2 F_2}{\partial z_4 \partial z_5}(Q_p^0, \omega_p^*) \right], \\ &= -v_2u_5(u_2 + u_3 + u_4) \frac{\omega_p^* \nu}{S_0} < 0. \end{aligned}$$

Let us now compute b , defined in assumption A_2 of theorem A.1, for system (A.8):

$$b = \sum_{k,i=1}^5 v_k u_i \frac{\partial^2 F_k}{\partial z_i \partial \omega_p}(Q_p^0, \omega_p^*).$$

The only term that is non null corresponds to:

$$\frac{\partial^2 F_2}{\partial z_5 \partial \omega_p}(Q_p^0, \omega_p^*) = \frac{\nu}{S_0}.$$

Substituting this term into the expression of b , one obtains:

$$\begin{aligned} b &= v_2u_5 \frac{\partial^2 F_2}{\partial z_5 \partial \omega_p}(Q_p^0, \omega_p^*) \\ &= v_2u_5 \frac{\nu}{S_0} > 0. \end{aligned}$$

Thus, $a < 0$ and $b > 0$. Using Theorem A.1, we conclude that when bifurcation parameter changes from $\omega_p < \omega_p^*$ to $\omega_p^* < \omega_p$, *i.e.* the basic reproduction number changes from $\mathcal{R}_0^{(p)} < 1$ to $\mathcal{R}_0^{(p)} > 1$, the DFE changes from GAS to unstable. Moreover, when the basic reproduction number is close to one, the endemic equilibrium Q_p^* appears and is locally asymptotically stable. This completes the proof. \square

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